

Mini Review

Diurnal Temperature Fluctuations and Mechanical Manipulation Affect Plant Stem Elongation¹

John E. Erwin², Royal D. Heins³, William Carlson³, and Shawn Newport⁴

INTRODUCTION

Commercial management of plant stem elongation relies heavily on the use of synthetic plant growth retardants. Concern over the impact of these compounds on the environment and human health has limited their use and may limit their availability (Bidinotto, 1990). As a result, methods for manipulating plant stem elongation which do not involve the application of chemicals must be developed. Environmental and mechanical manipulation can affect plant stem elongation and may provide commercially acceptable methods for stem elongation control.

Height Control Using Temperature Manipulations

Went (1952; 1957) showed that plant stem elongation was affected by day temperature (DT) and night temperature (NT). *Lycopersicum* stem elongation increased as DT increased and NT decreased (Went, 1944). Similar findings were found on *Fuchsia* (Tageras, 1979), *Dendrathema* (Karlsson, 1988), *Lilium* (Erwin et al., 1989a; Erwin and Heins, 1990), and *Campanula* (Moe et al., 1991) (Fig. 1). Erwin et al. (1989a) and Erwin and Heins (1990) showed that the effects of temperature on *Lilium* stem elongation could be best described by the relationship between DT and NT rather than actual DT and NT between 10 and 30 C (Fig. 2). Stem elongation on *Lilium longiflorum* increased as the difference (DIF) between DT and NT ($DIF = DT - NT$) increased (Fig. 3). Similar results were found on *Dendranthema* (Karlsson et al., 1989), *Euphorbia* (Berghage, 1989; Berghage and Heins, 1990), *Xanthium* (Erwin, 1991), *Streptocarpus* (Erwin, 1991), *Campanula* (Moe et al., 1991),

¹Received for publication Dec. 19, 1991 and in revised form Jan 29, 1992.

²Asst. Prof., Dept. of Hortic. Sci., Univ/Minnesota, St. Paul, MN 55108.

³Prof., Dept. of Hortic., Michigan State Univ., E. Lansing, MI 48824.

⁴Graduate Res. Asst., Dept. of Hortic., Michigan State Univ., E. Lansing, MI 48824.
(Editor's note: This review is an adaptation of Symposium I - "Regulation of Growth in Greenhouse Crops", presented by the authors at the 1991 PGRSA meeting).

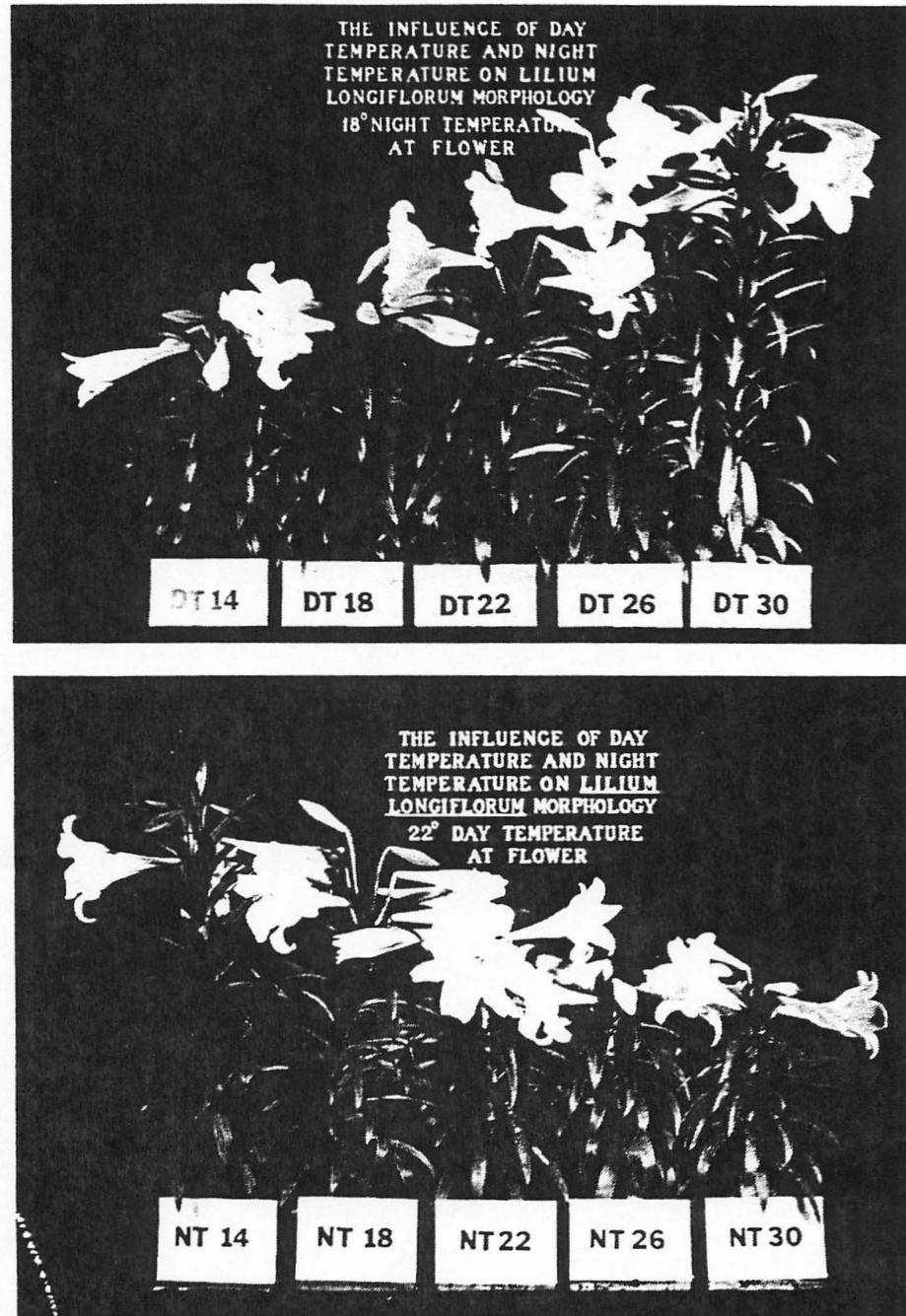


Figure 1. The effect of increasing day temperature (top) and increasing night temperature (bottom) on the height of *Lilium longiflorum* Thunb. cv 'Nellie White' at anthesis. Plants grown at higher average daily temperatures flowered earlier than plants grown at cooler average daily temperatures. As plants grown at higher average daily temperatures reached anthesis, they were placed in a cooler (4 C) until plants grown at cooler temperatures reached anthesis. Stem elongation did not occur in the cooler. When all plants had reached anthesis, the photograph was taken. Internode number was not significantly different among plants (Heins and Erwin, 1990).

Temperature fluctuations and mechanical manipulation affect stem elongation

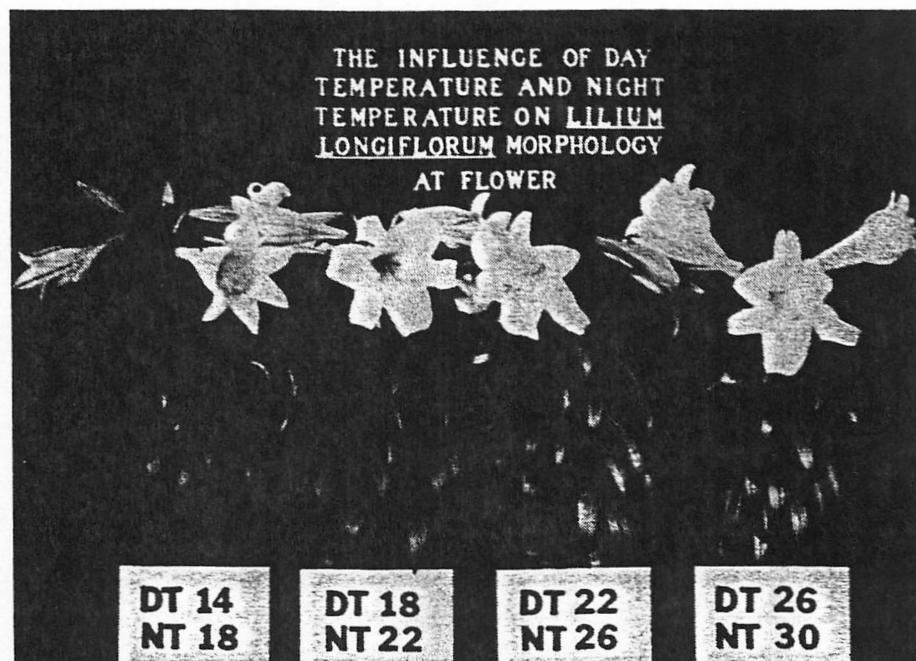


Figure 2. Appearance of *Lilium longiflorum* Thunb. cv 'Nellie White' at anthesis when grown under 4 temperature regimes with day temperatures (DT) 4 C cooler than night temperatures (NT). Plants grown at higher average daily temperatures flowered earlier than plants grown at cooler average daily temperatures. As plants grown at higher average daily temperatures reached anthesis, they were placed in a cooler (4 C) until plants grown at cooler temperatures reach anthesis. Stem elongation did not occur in the cooler. When all plants had reached anthesis, the photograph was taken. Internode number was not significantly different among plants (Erwin et al., 1989a).

and *Fuchsia* (Erwin et al., 1991a) (Fig. 4). The only group of plant species studied which did not respond to DIF were spring bulbous crops (*Tulipa*, *Narcissus*, and *Hyacinth*) (Heins and Erwin, 1990). While original research by Went (1957) suggested that plant stem elongation was primarily influenced by DT, measurements of internode lengths from his published photographic plates of *Pisum sativum* plants grown by Went showed internode length was indeed strongly correlated with DIF.

Temperature also strongly influences leaf expansion (Dale, 1964; 1965; Milthorpe, 1959). Dale (1964) showed that *Phaseolus vulgaris* leaf expansion was greatest when DT and NT were constant, i.e. a 0 C DIF. Reexamination of Dale's data (1964) showed this conclusion was based on a number of environmental treatments which contained either a 30 C DT and/or NT. Based on Dale's own data and conclusions, leaf expansion was inhibited by 30 C temperatures. Therefore, conclusions relating temperature effects on leaf expansion based on 30 C temperature treatments may be misleading. If

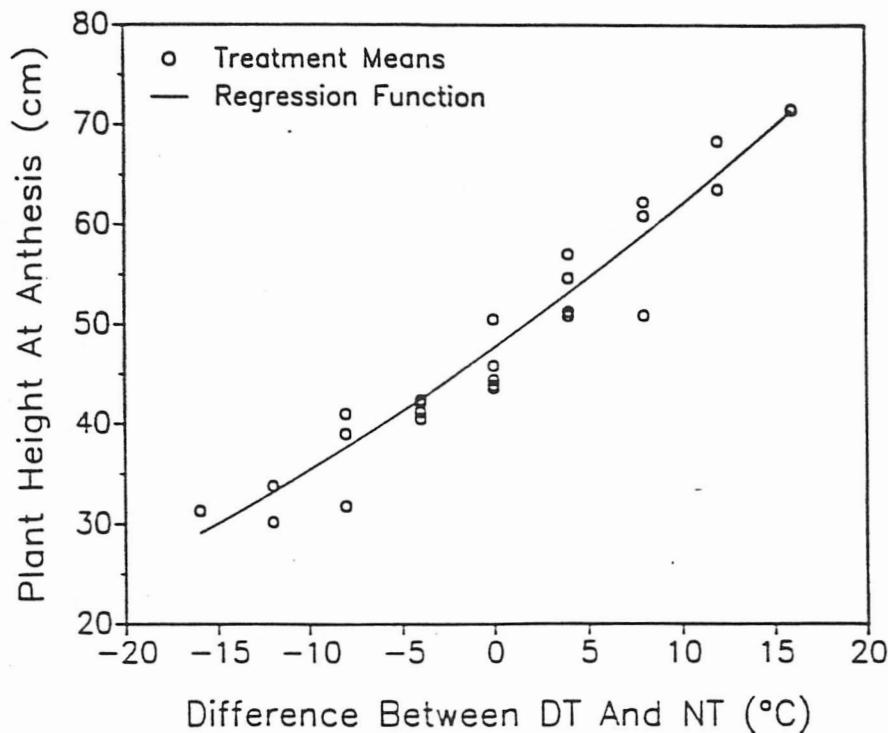


Figure 3. Relationship between *Lilium longiflorum* Thunb. cv 'Nellie White' plant height at anthesis and the difference (DIF) between the day temperature (DT) and the night temperature (NT). Squares represent mean plant heights for each treatment. The solid line represents the regression function $1.4860 * \text{DIF} - 0.0416 * \text{DT} * \text{NT} + 1.9139 * \text{AVG TEMP} + 25.661$ ($r^2=0.84$). The regression line also represents the effect of both day temperature and night temperature by night temperature interaction and the effect of average temperature on final height. Internode number was not significantly different among plants (Erwin et al., 1989a).

Dale's data from environments not containing a 30°C DT or NT are eliminated, leaf area increased as DIF increased. A positive correlation between DIF and leaf expansion has also been noted on *Fuchsia* (Erwin et al., 1991a).

Anatomical studies on *Lilium longiflorum* grown under different DT/NT regimes showed that plant stem elongation and leaf expansion responses to

DIF were due to cellular elongation and not division (Erwin et al., 1991c) (Fig. 5). Cell elongation increased as DIF increased (Fig. 5, top). Cell width was unaffected by DIF (Fig. 5, bottom).

The basis for the effect of DIF on cell elongation is believed to involve gibberellin (Zieslin and Tsujita, 1988;

Temperature fluctuations and mechanical manipulation affect stem elongation

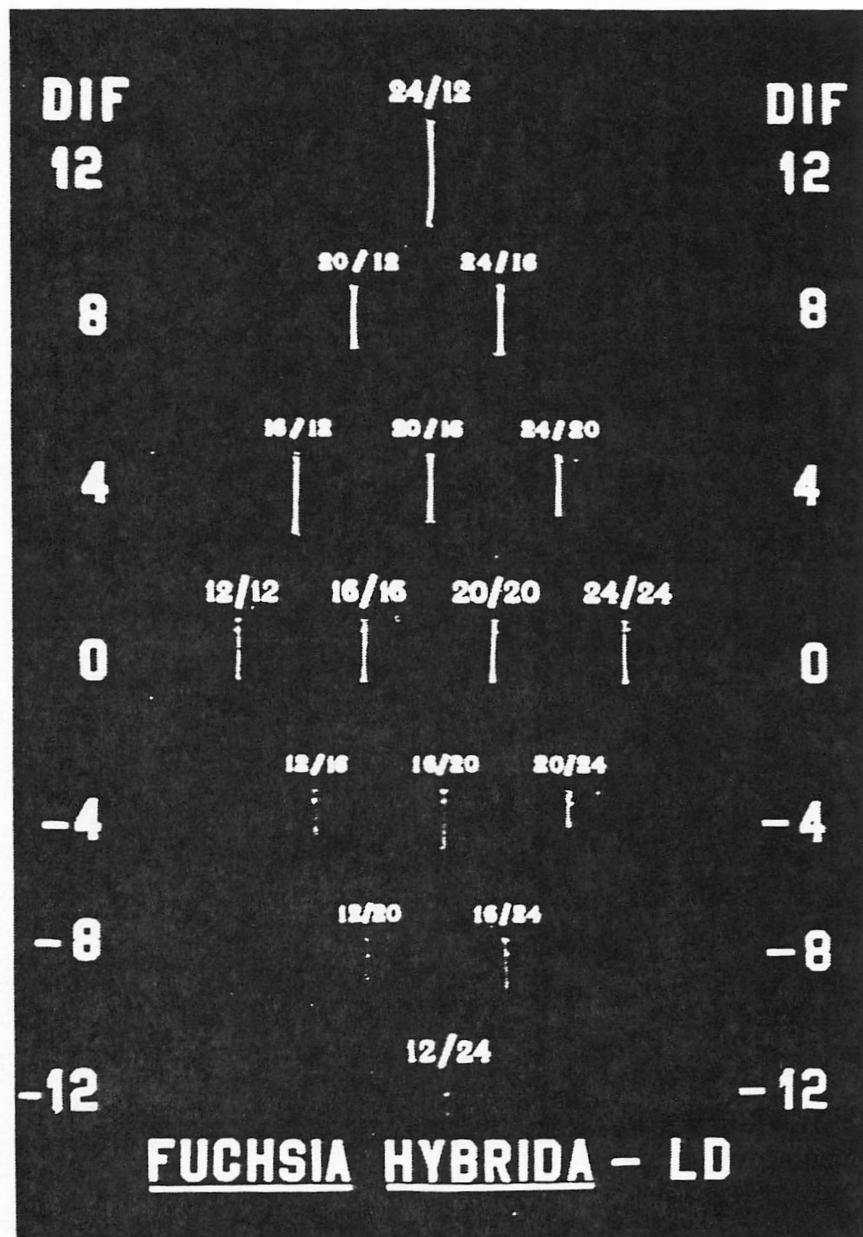


Figure 4. Effect of DIF between DT and NT (DT-NT) on internode length of *Fuchsia x hybrida* cv 'Dollar Princess'. Plants were grown under LD conditions, i.e. a 9-h 15-min photoperiod plus a 4-h NI using incandescent lighting at an irradiance of $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Erwin et al., 1991a).

Erwin et al.

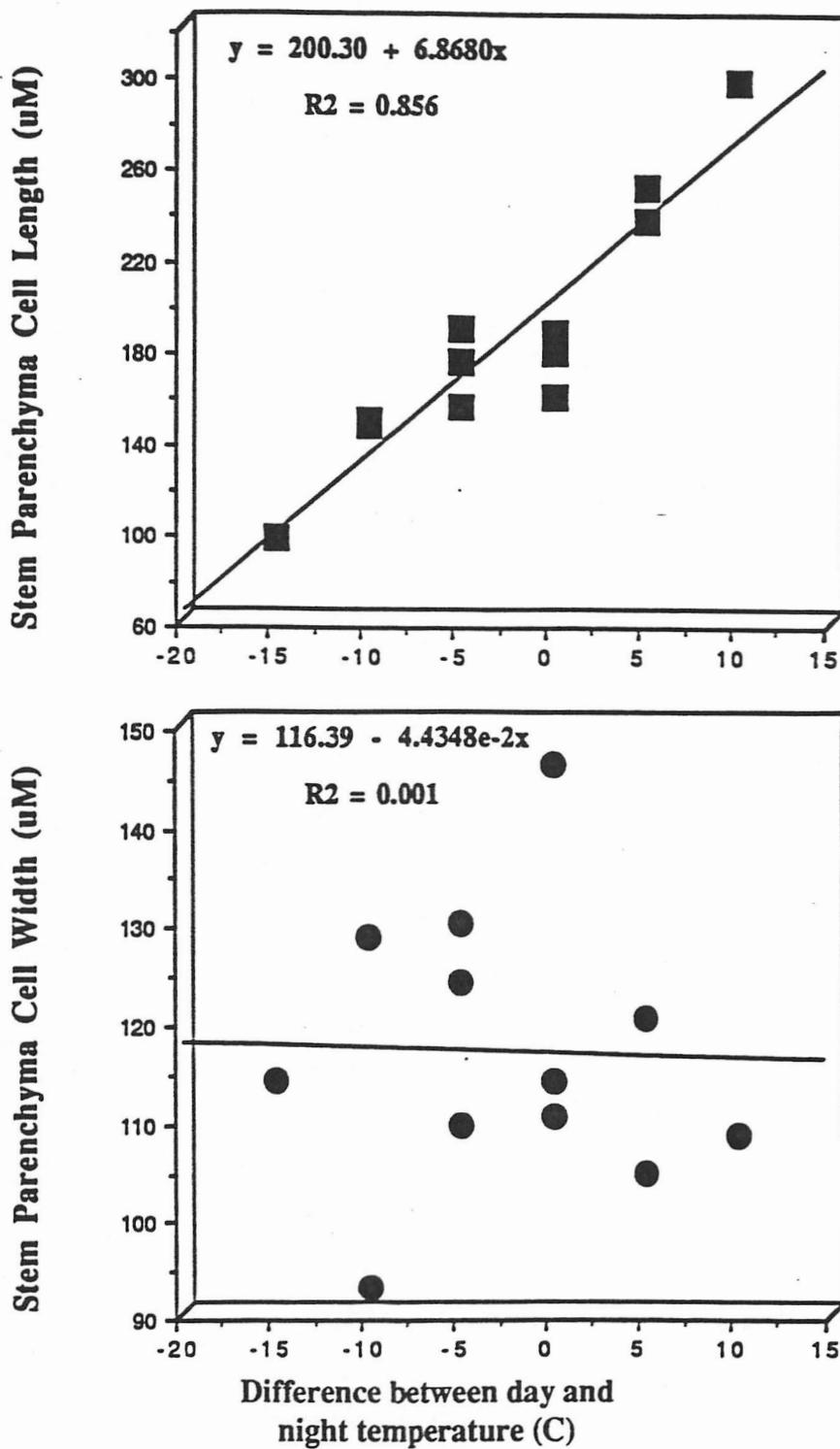


Figure 5. The effect of the difference (DIF) between day (DT) and night (NT) temperature (DT-NT) on *Lilium longiflorum* cv 'Nellie White' central parenchyma cell length (top) and width (bottom) (Erwin and Heins, 1991c).

Temperature fluctuations and mechanical manipulation affect plant elongation

Erwin et al., 1989a; Moe and Heins, 1990; Moe et al., 1991; Erwin, 1991). Application of gibberellin₄₊₇ (GA₄₊₇) to *Lilium* bulbs prior to planting overcame subsequent inhibition of stem elongation during the forcing stage in a negative DIF environment (Zieslin and Tsujita, 1988). Similarly, Moe et al. (1991) showed that foliar application of GA₃ overcame inhibition of *Campanula isophylla* stem elongation when plants were grown in a negative DIF environment. Similar stimulation of elongation in a -DIF environment by GA₄₊₇ is seen with *Lycopersicum* (Erwin and Pierson, personal communication). In contrast, application of a GA biosynthesis inhibitor, ancymidol (α -cyclopropyl- α -(4-methoxyphenyl)-5-pyrimidinemethanol), resulted in a greater percent decrease in *Lilium* stem elongation of positive DIF grown compared to negative DIF grown plants (Erwin et al., 1989a). A correlation between DIF and endogenous GA levels effects on stem elongation is, therefore, apparent.

Supportive evidence for GA involvement in DIF effects on stem elongation can be seen in temperature effects on plant sex expression in dioecious plants. Both GA (Jones and Zeevaart, 1980; Pharis and King, 1985) and DIF (Erwin, 1991) can affect plant sex expression. Application of gibberellins to *Agrostemma* induces maleness (Jones and Zeevaart, 1980). In contrast, application of GA biosynthesis inhibitors induces femaleness in muskmelon

(Halevy and Rudich, 1967; Pharis and King, 1985). *Cucurbitaceae* grown in a +DIF environment have significantly more male flowers than female flowers (Fig. 6). Conversely, plants grown under a 0 or a -DIF environment have equal or more female flowers than male flowers (Erwin, 1991). Although other factors such as ethylene can influence flower sex expression in *Cucurbitaceae*, these results combined with previous data provide additional evidence for GA involvement in plant responses to DIF.

Photoperiod interacts with DIF to affect plant stem elongation (Erwin et al., 1991a; Berghage et al., 1991). Independent of temperature, stem elongation increases as photoperiod length increases on *Fuchsia* (Vince-Prue, 1977). Plant stem elongation responses to DIF decrease as photoperiod length increases. The reduction in response to DIF as photoperiod increases occurs whether the photoperiod is extended via night interruption lighting (Erwin et al., 1991a) or by day extension lighting (Berghage, unpublished data) (Fig. 7).

Light intensity interacts with DIF to affect plant stem elongation. Plant responses to DIF increase as irradiance increases (Berghage, unpublished data).

Light quality interacts with DIF to affect stem elongation (Moe and Heins, 1990; Erwin, 1991; Moe et al., 1991). In

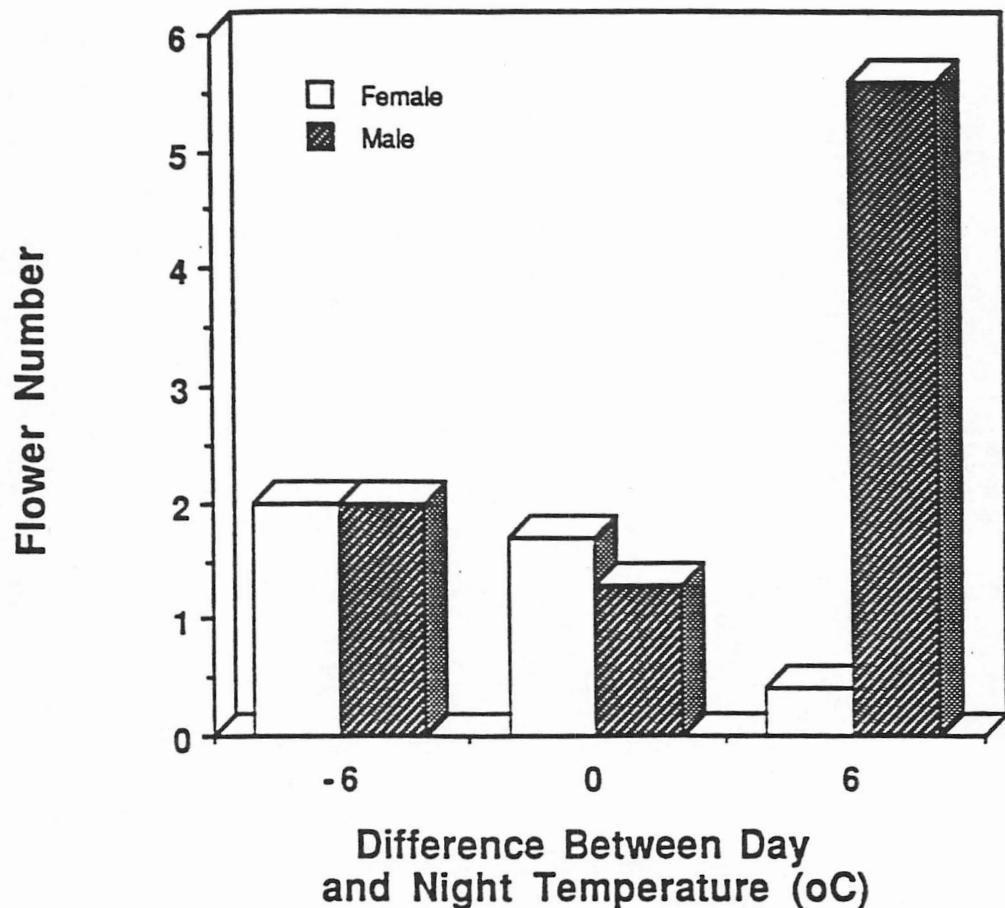


Figure 6. The effect of the difference (DIF) between day (DT) and night (NT) temperature on *Cucurbita* cv 'Tay-Belle' flower sex expression. Data were collected 60 days after germination. Thermoperiod and photoperiod length were 12 hours. Temperature treatments were 17 day/23°C night (-6 DIF), 20 day/20°C night (0 DIF), or 23 day/17°C night (+6 DIF) (Erwin, 1991).

specific, there is an interaction between phytochrome photoequilibria and DIF effects on stem elongation. Red light has been shown to reduce stem elongation whereas far red light promotes stem elongation (Smith, 1986). Far red light overcomes the reduction in stem elongation of *Campanula* (Moe et al., 1991) and *Fuchsia* (Erwin, 1991) grown in a negative DIF environment. Conversely, red light enhances inhibition of stem elongation by -DIF environments in *Cam-*

panula when plants are exposed to the red light during the night (Moe et al., 1991) and when plants are exposed to red light during the day on *Fuchsia* (Erwin, unpublished data). *Fuchsia* stem elongation is enhanced by exposure of plants to either red or far red lighting during the night (Erwin, 1991). Interestingly, in the case of *Fuchsia*, red light and GA₄₊₇ appear to act synergistically to affect stem elongation responses to diurnal

Temperature fluctuations and mechanical manipulation affect plant elongation

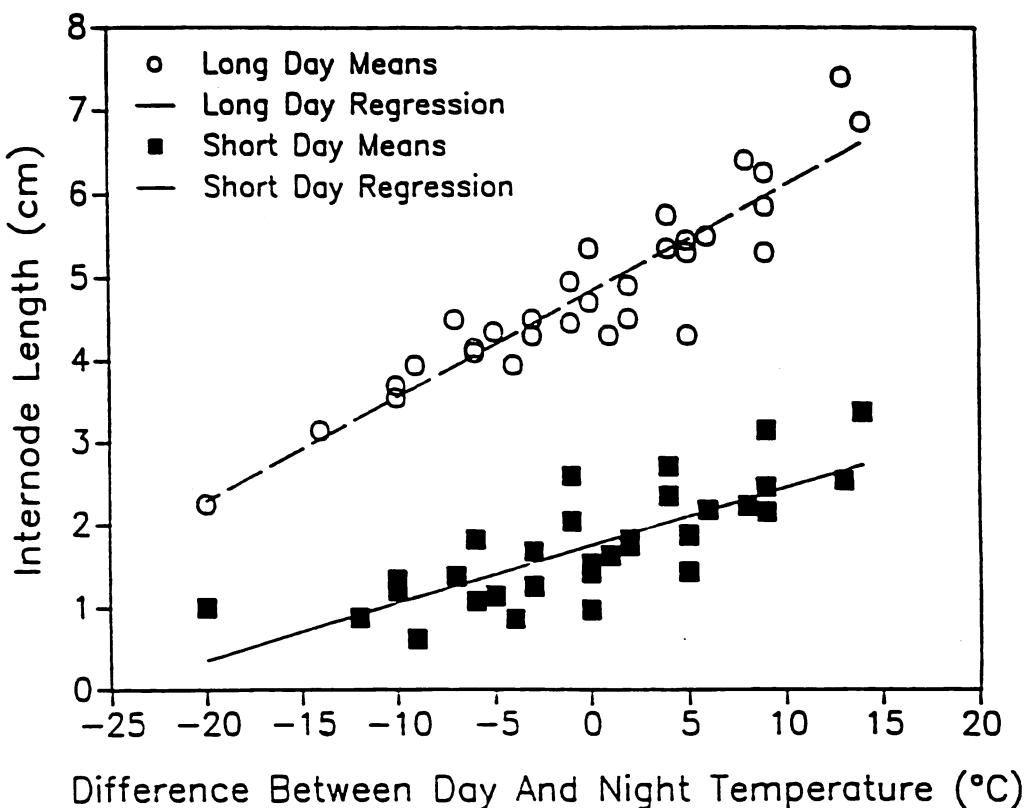


Figure 7. Effect of DIF between DT and NT (DT-NT) on internode length of *Fuchsia x hybrida* 'Dollar Princess' plants grown under LD (9-h 15-min photoperiod plus 4-h NI using incandescent lamps at an irradiance of $2 \mu\text{mol m}^{-2} \text{s}^{-1}$) and SD (9-h 15-min photoperiod). Data were normalized across 1988 and 1989 experiments within photoperiod treatments. Regression function calculated from LD data was: internode length (cm) = $4.727 + (0.129 \times X)$ ($r^2 = 0.87$); from SD data was; internode length (cm) = $1.871 + (0.071 \times X)$ ($r^2 = 0.64$) (Erwin et al., 1991a).

fluctuations in temperature (Erwin, 1991) (Fig. 8). These data suggest that phytochrome may be involved in plant stem elongation responses to diurnal temperature fluctuations. Experimentation is currently underway to determine the degree of phytochrome involvement in plant stem elongation responses to temperature fluctuations.

The potential effects of blue lighting on plant responses to DIF are unknown. However, preliminary data suggest that

supplemental blue lighting during the day reduces stem elongation but does not interact with DIF (Erwin, observation).

Plant stem elongation is not constant during a day/night cycle (Went, 1952; Erwin and Heins, 1988). Instead, the rate of plant stem elongation decreases during the photoperiod and increases during the nyctoperiod (Fig. 9). Therefore the rate of stem elongation is greatest at the end of the nyctoperiod and the

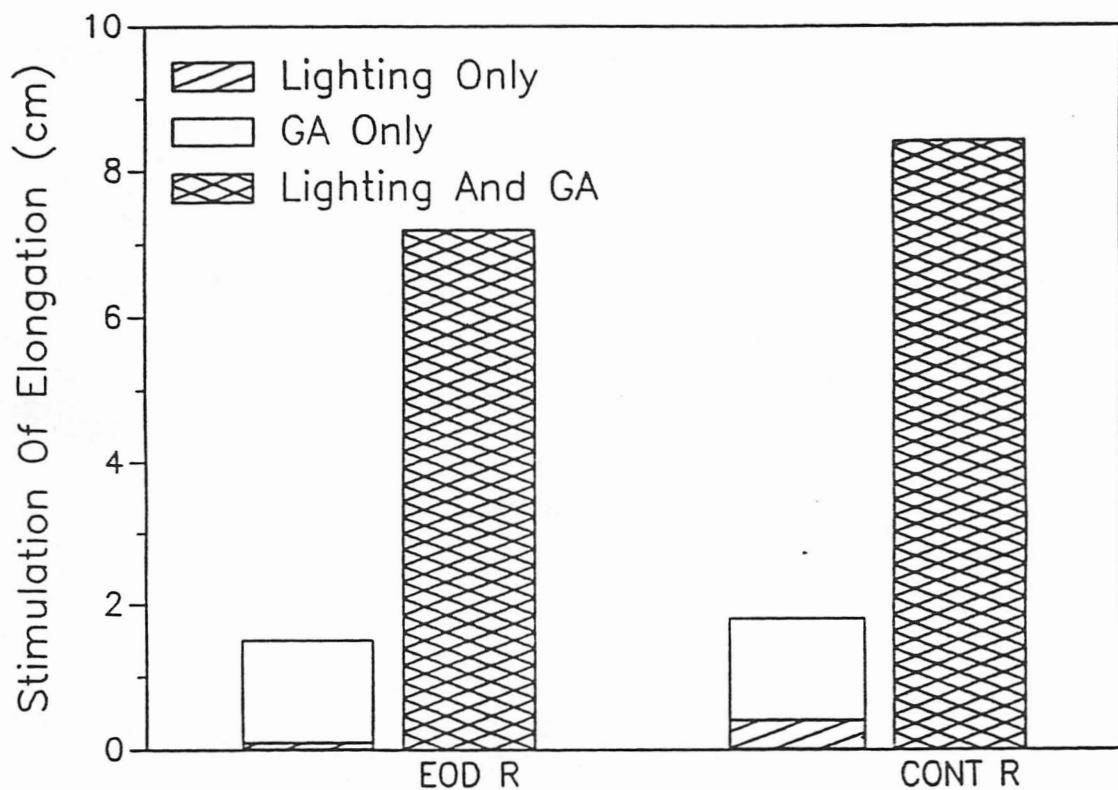


Figure 8. Comparison of the increase in second internode length of *Fuchsia x hybrida* cv 'Dollar Princess' grown with a cooler day temperature than night temperature (17 C day temperature/23 C night temperature) resulting from red lighting only, application of GA_{4+7} only, or red lighting plus application of GA_{4+7} . GA_{4+7} was applied at a rate of 10 ppm until the foliage was moist (Erwin, 1991). Plants were exposed to red lighting as an EOD (end-of-day) treatment (first 3 hours of the night) or as a CONT (continuous) (all night) treatments. The 2 bars on the left show absolute increases in elongation from the GA only treatment plus the lighting only treatment. The 2 bars on the right show the stimulation in elongation resulting from lighting treatment and GA treatment applied simultaneously to the plants.

Temperature fluctuations and mechanical manipulation affect plant elongation

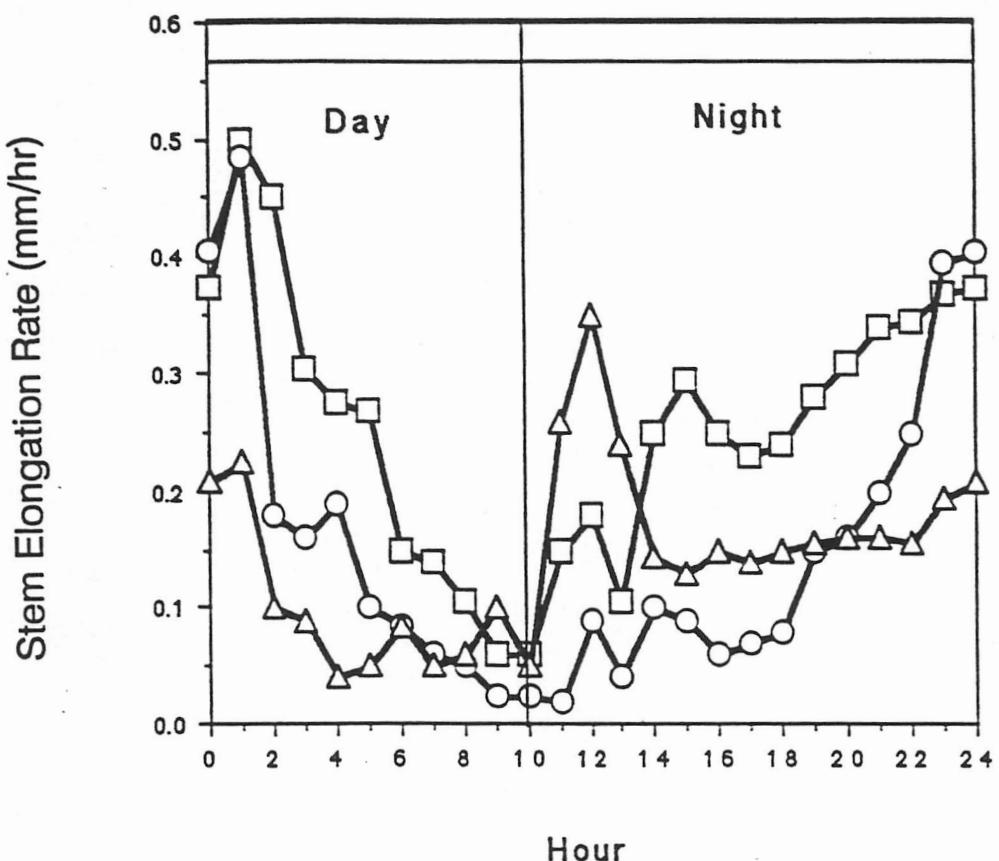


Figure 9. The effect of photoperiod and nyctoperiod on the rate of *Dendranthema grandiflora* cv 'Bright Golden Anne' stem elongation rate. Data presented are means over a 3 day period. Data were collected every 5 minutes. Hourly means were then calculated. Data collection was through the use of an angular displacement transducer (ADT) connected to a computer. The system had a resolution of 2 mn per 5 minute period. Squares, circles, and triangles represent hourly treatment means of the stem elongation rate of plants grown with a higher day temperature than night temperature (23 C day/17 C night temperature), equal day and night temperature (20 C day/20 C night temperature), and cooler day than night temperature (17 C day/23 C night temperature, respectively (Erwin and Heins, in press).

beginning of the photoperiod. This information lead us to study whether plant stem elongation is sensitive to temperature fluctuations during the last 2 hours of the night and the first 2 hours of the day. We found that plant stem elongation was very sensitive to temperature fluctuations during the first 2

hours of the day (Erwin et al., 1989b; Heins and Erwin, 1991) (Fig. 10). Dropping temperatures during the first 2 hours of the morning to below the night temperature was almost as effective in inhibiting stem elongation as dropping temperatures during the entire day.

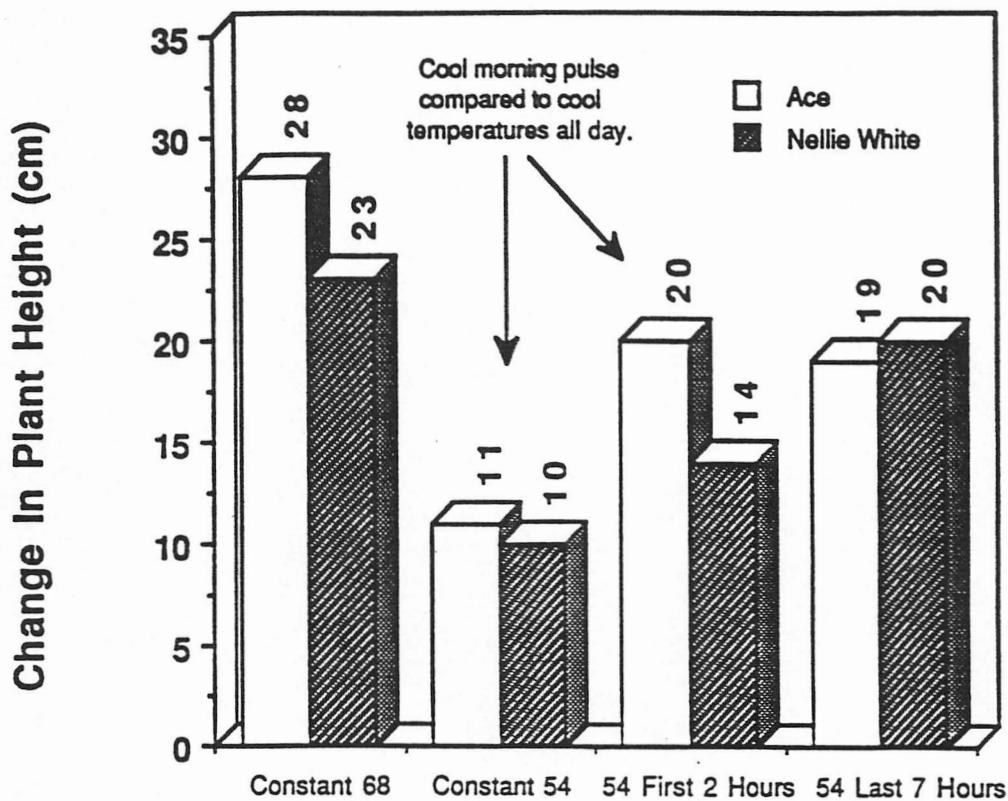


Figure 10. The effect of temperature fluctuations at different times of the day on *Lilium longiflorum* cv Nellie White' stem elongation. The uppermost leaf was marked after flower initiation upon placement of plants into the different temperature environments. Plant height was then measured at anthesis. The change in plant height is presented in the figure as the numerals above each histogram bar. Differences in leaf number among treatments were not significant (Heins and Erwin, 1991).

Both leaf orientation (Erwin et al., 1989a) and chlorophyll content (Erwin et al., 1991b; Berghage et al., 1991) are affected by DIF. Leaf orientation increased as DIF increased from -16 to 16 C (Erwin et al., 1989a). Leaf orientation is defined as the angle of the leaf relative to a line perpendicular to the stem axis. Therefore, the position of the leaf becomes more upright, i.e. leaf orientation increases as DIF becomes more positive. Leaf chlorophyll con-

tent also increases linearly as DIF increases from -10 to 10 C (Fig. 11 (Erwin et al., 1991b).

Responses to DIF are rapid. Most plants respond to a change in day and night temperatures within 24 hours (Heins and Erwin, 1990). The absolute response of plant stem elongation is greatest when a plant is elongating most rapidly (Berghage, 1989).

Temperature fluctuations and mechanical manipulation affect plant elongation

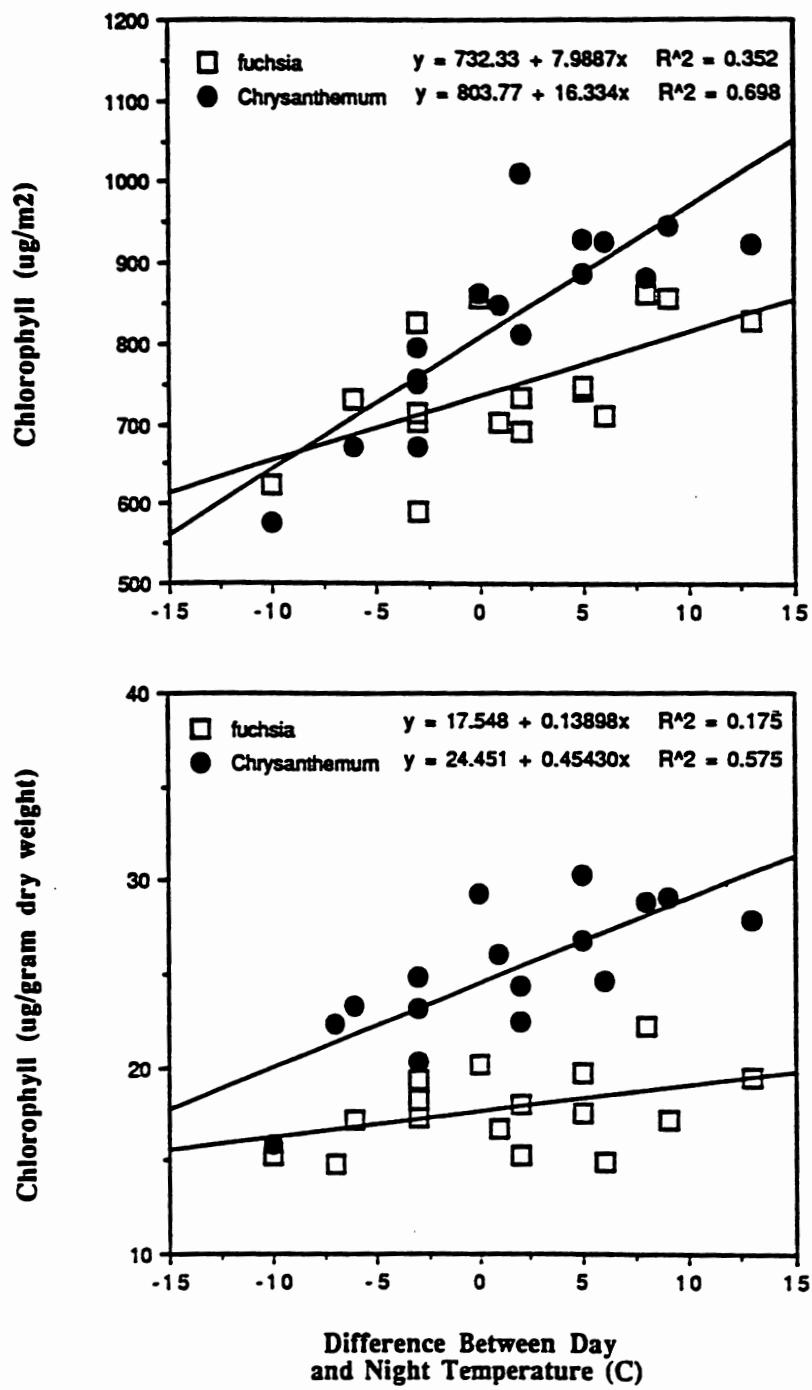


Figure 11. The effect of the difference (DIF) between day (DT) and night (NT) temperature (DT-NT) on total chlorophyll content expressed on a per unit area (top) and a per unit dry weight basis (bottom) (Erwin and Heins, 1991b).

Height Control Methods Using Water Stress and Mechanical Shaking

Mechanical stress reduces stem elongation, affects plant appearance, may delay flowering, and may affect the rate of plant development. One of the earliest documentation of the effects of mechanical stress on plant growth was that of the German botanist Metzger. Metzger was able to show that plant height was reduced as a result of mechanical stress due to wind. Jaffe (1973) termed inhibition of stem elongation to tactile mechanical stress as thigmomorphogenesis. In contrast, inhibition of stem elongation resulting from nontactile mechanical stress was termed seismomorphogenesis (Mitchell et al., 1975). *Lilium* elongation was reduced by 30% after plants were shaken twice a day for 10 seconds (Miller, 1991). Similarly, brushing tomato transplants reduced seedling stem elongation by 37% (Latimer and Thomas, 1991). Reduction in stem elongation was also shown to reduce stem elongation of *Hordeum*, *Bryonia*, *Cucumis*, *Phaseolus*, and *Ricinus* (Jaffe, 1973). In contrast, *Cucurbita*, *Pisum*, and *Triticum* stem elongation was unaffected by rubbing. Complete reviews of the effects of mechanical stress on plant growth have been published by Biddington (1986) and Latimer (1991).

Plant height can also be controlled using water stress as a management

technique. Water stress was one of the earliest and common techniques to control plant stem elongation in greenhouses prior to the advent of plant growth retardants. In contrast to mechanical stress, water stress is believed to reduce plant stem elongation by simply reducing the force which drives cellular elongation, i.e. turgor pressure.

In a recent experiment we studied how mechanical stress, water stress, and the day/night temperature regime plants were grown under interacted to affect *Lycopersicum* stem elongation. *Lycopersicum* plants shaken at a rate of 125 rpm for 10 minutes each day were 14 and 6% shorter than untreated plants when grown under +DIF and -DIF environments. Water-stressed were 24% shorter than unstressed plants when plants were grown in a +DIF environment and 28% shorter when plants grown in a -DIF environment (Table I). There was no significant impact of the day/night temperature environment on elongation responses to the imposed stress treatments (Table I).

Water stress and seismotropic effects on plant stem elongation were not additive. The lack of additivity suggests that these 2 methods may be acting through different methods with respect to their reduction of plant stem elongation. This was not unexpected as mechanical and water stress have been documented to differ in the way

Temperature fluctuations and mechanical manipulation affect plant elongation

in which they reduce plant stem elongation. Equally interesting, is the lack of an interaction between the temperature environment which plants are grown under and water and mechanical stress on plant stem elongation. The

lack of interaction suggests that day/night temperature regime effects on plant stem elongation may be independent of mechanical and/or water stress effects on cellular elongation.

Table I. The effect of day/night temperature regime, water stress, and shaking on *Lycopersicum esculentum* seedling height after 5 weeks. Day/night temperature regimes were either 20/15 C (day/night temperature) (+DIF) or 15/20 C (-DIF). Water stress was defined as 50% of the total media water capacity. The seismotropic treatment was delivered by turning plants at a rate of 125 rpm for 10 minutes each day compared to control plants which were not moved.

Physical treatment	Treatment regime	
	+DIF	-DIF
Untreated	133*	120
Water stress	101 (-24%) ^b	86 (-28%)
Seismotropic stress	115 (-14%)	113 (-6%)
Water + seismotropic stress	100 (-25%)	78 (-35%)

*Total plant height expressed in millimeters.

^bPercent change in height relative to untreated plants.

LITERATURE CITED

- Berghage RD 1989 Modeling stem elongation in *Euphorbia pulcherrima*. PhD Thesis. Michigan State University
- Berghage RD and RD Heins 1991 Quantification of temperature effects on stem elongation in poinsettia. J Amer Soc Hortic Sci 116:14-18
- Berghage RD, JE Erwin, and RD Heins 1991 Photoperiod influences leaf chlorophyll content in chrysanthemum grown with a negative DIF temperature regime. Hortscience 26:92
- Biddington NL 1986 The effects of mechanically-induced stress in plants-a review. Plant Growth Reg 4:103-123
- Bidinotto RJ 1990 The great apple scare. Reader's Digest, October, pages 53-58
- Dale JE 1964 Some effects of alternating temperature on the growth of French bean plants. Ann Bot, NS 28:127-135
- Dale JE 1965 Leaf growth in *Phaseolus vulgaris*, II. Temperature effects and the light factor. Ann Bot 29:293-308

Erwin et al.

- Erwin JE and RD Heins 1988 Effect of diurnal temperature fluctuations on stem elongation circadian rhythms. HortScience 23:820
- Erwin JE, RD Heins, and MG Karlsson 1989a Thermomorphogenesis in *Lilium longiflorum*, Thunb. Am J Bot 76:47-52
- Erwin JE, RD Heins, RD Berghage, BJ Kovanda, WH Carlson, and JA Biernbaum 1989b Cool mornings can control plant height. Growertalks 52(9):73-74
- Erwin JE and RD Heins 1990 Temperature effects on lily development rate and morphology from the visible bud stage until anthesis. J Amer Soc Hortic Sci 115:644-646
- Erwin JE 1991 Thermomorphogenesis in plants. PhD Thesis, Michigan State University
- Erwin JE, RD Heins, and R Moe 1991a Temperature and photoperiod effects on *Fuchsia x hybrida* morphology. J Amer Soc Hortic Sci 116:955-960
- Erwin JE, RD Berghage, and RD Heins 1991b Circadian temperature effects on plant chlorophyll content. HortScience 26:105
- Erwin JE, P Velguth, and RD Heins 1991c Diurnal variations in temperature affect cellular elongation but not division. HortScience 26:105
- Halevy AH and J Rudich 1967 Modification of sex expression in muskmelon by treatment with the growth retardant B-995. Physiol Plant 20:1052-1058
- Heins RD and JE Erwin 1990 Understanding and applying DIF. Greenhouse Grower 8(2):73-78
- Heins RD and JE Erwin 1991 The history of DIF and the use of a morning temperature dip to control plant height. Minn Comm Flower Growers Bull 40(6):1-4
- Jaffe MJ 1973 Thigmomorphogenesis: The response of plant growth and development to mechanical stimulation. Planta 114:143-157
- Jones MG and JAD Zeevaart 1980 The effect of photoperiod on the levels of seven endogenous gibberellins in the long-day plant *Agrostemma githago* L. Planta 149:274-279
- Karlsson MG 1988 Temperature and irradiance effects on *Dendranthema grandiflorum* cv 'Bright Golden Anne' growth and development. PhD Thesis, Michigan State University
- Karlsson MG, RD Heins, JE Erwin, RD Berghage, WH Carlson, and JA Biernbaum 1989 Temperature and photosynthetic photon flux influence chrysanthemum shoot development and flower initiation under short-day conditions. J Amer Soc Hortic Sci 114:158-163
- Kaczperski MP 1989 Influence of temperature and irradiance on growth and development of *Petunia x hybrida* 'Snow Cloud'. Master's Thesis, Michigan State University
- Latimer JG 1991 Mechanical conditioning for control of growth and quality of vegetable transplants. HortScience 26:1456-1461
- Latimer JG and PA Thomas 1991 Application of brushing for growth control of tomato transplants in a commercial setting. Hortech 1:109-110

Temperature fluctuations and mechanical manipulation affect plant elongation

- Miller W 1991 Try mechanical stress as a "natural" growth regulator. GrowerTalks 55(7):81-85
- Milthorpe FL 1959 Studies on the expansion of the leaf surface. I. The influence of temperature. J Exp Bot 10:233-249
- Mitchell CA, CJ Severson, JA Wott, and PA Hammer 1975 Seismomorphogenic regulation of plant growth. J Amer Soc Hortic Sci 100:161-165
- Moe R and RD Heins 1990 Control of plant morphogenesis and flowering by light quality and temperature. Acta Hortic (in press)
- Moe R, RD Heins, and JE Erwin 1991 Effect of day and night temperature alterations, and plant growth regulators on stem elongation and flowering of the long-day plant *Campanula isophylla* Morettii. Scientia Hortic 48:141-151
- Pharis RP and RW King 1985 Gibberellins and reproductive development in seed plants. Annu Rev Plant Physiol 36:517-568
- Smith H 1986 The perception of the light environment. Pages 187-218 In RE Kendrick and GHM Kronenberg, Eds, Photomorphogenesis In Plants. Martinus Nijhoff Pub, Boston, Mass
- Tageras H 1979 Modifying effects of ancymidol and gibberellins on temperature induced elongation in *Fuchsia x hybrida*. Acta Hortic 91:411-417
- Vince-Prue D 1977 Photocontrol of stem elongation in light-grown plants of *Fuchsia x hybrida*. Planta 133:141-156
- Went F 1944 Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. Amer J Bot 31:135-15
- Went FW 1952 The effect of temperature on plant growth. Annu Rev Plant Physiol 4:347-362
- Went FW 1957 The experimental control of plant growth. Chr Bot 17 Pages 1-126. The Ronald Press Co, NY, NY
- Zieslin N and MJ Tsujita 1988 Regulation of stem elongation of lilies by temperature and the effect of gibberellin. Scientia Hortic 37:165-169